THE BIOLOGY OF CALANUS FINMARCHICUS IN THE GULF OF MAINE AND BAY OF FUNDY

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Introduction and Methods

The problem considered in the present paper concerns the production and dispersal of *Calanus finmarchicus* in a partially enclosed body of water. There have been two principal objectives; first, a determination of the breeding seasons, annual number of broods, rate of growth and length of life; second, an evaluation of different spawning areas, and dispersal of eggs and larvæ.

Monthly cruises were made from July 28, 1931 to September 29, 1932 in the Bay of Fundy and from April to September, 1932, in the inner part of the Gulf of Maine, with one cruise in the outer Gulf and along the south coast of Nova Scotia, yielding in all a total of 838 zoöplankton samples (Fig. 1). In August 1931 one line of stations was taken in the Gulf.[2]

For convenience in description, the region has been subdivided into four areas shown in Fig. 1. For the sampling of eggs and immature stages, the pump was used during the summer, a volume of 250 liters of water from each of four levels, 0, 10, 30, and 50 meters being filtered at each station. Analyses were made by the Sedgewick-Rafter counting method, and the number of individuals per cubic meter calculated. In determining horizontal distribution, in the present report, the value taken for each station represents the mean of the four levels. Until weather conditions permitted the use of the pump (end of June), half-meter nets (two meters in length) of No. 10 silk were utilized. The hauls were of 15 minutes duration and were oblique from 50 meters to the surface, the distance being divided into six steps at intervals of 10 meters each. The counts were made by the same method used in the pump samples, but the number of organisms per minute of towing was taken as the unit of measure.

Importance

Calanus finmarchicus is the most abundant animal in the Gulf of Maine, occurring offshore throughout the year and well into inshore

[1] Contribution No. 85.

[2] Investigations for the International Passamaquoddy Fisheries Commission.

waters except during the warm summer months when its distribution is somewhat variable. In Frenchmans Bay, with temperatures as low as 7–9° C. persisting in the lower levels, it was found abundant throughout the summers of 1929, 1930, and 1932, but in shallower or more turbulent estuarine areas such as Passamaquoddy Bay, where the

FIGURE I

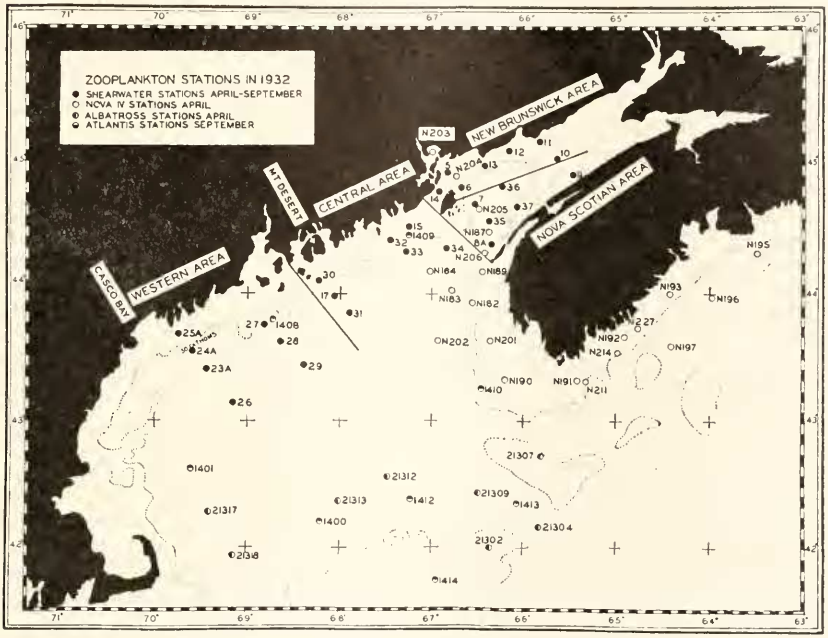

FIG. 1. Zoöplankton stations in 1932.

whole water mass responds more rapidly to seasonal warming (10–12° C. after August 1), *Calanus* was comparatively sparse between June and October.

Its importance in the region is indicated in Tables I and II giving the relative percentage by number of *C. finmarchicus* to the total zoöplankton population. Within the Bay of Fundy, *Calanus* was found most abundant at all times in the vicinity of the deep basin, with year values increasing upon approaching the entrance. Thus, as indicated below, at Station 5 in the Quoddy region the mean for the year was 32.4 per cent, at Station 6 east of Grand Manan 37 per cent, and at Station 8A near the mouth on the Nova Scotian side, 41.8 per cent.

In the Gulf of Maine the highest values occurred in the central area where production of many of the pelagic species breeding during the summer appears to be largely unsuccessful. Here *C. finmarchicus* ranged from 40 per cent to 90 per cent, except in April when locally spawned larvæ of *Balanus balanoides* dominated the hauls.

Bigelow (1926, p. 199) found that in the Gulf of Maine *Calanus* averaged approximately 55–60 per cent of the total copepod content. In 1932 it averaged 60.4 per cent of the zoöplankton population in May with a total copepod content of 77.2 per cent and 39.9 per cent for the period April to September. In the eastern Atlantic Ruud's (1929, p. 11) records indicate that off Möre in 1926 and 1927 *C. finmarchicus* formed about 13–15 per cent of the copepod population in March and rose to 63.4 per cent following vernal augmentation. The average for the period March–July during the two years was approximately 39 per cent.

TABLE I

Relative percentage by number of *C. finmarchicus* to the total zoöplankton population, 1931–32, Bay of Fundy.

1931–32	Bay of Fundy			
Month	Mean	Station 5	Station 6	Station 8A
September	28.5	17.5	6.7	61.4
October	23.4	23.4	—	—
November	31.3	36.1	34.6	23.3
December	37.9	61.2	34.2	18.2
January	25.9	25.9	—	—
March	61.6	73.2	57.3	54.4
April	34.8	49.7	36.6	18.1
May	41.0	4.8	56.7	61.5
June	36.4	15.5	42.5	51.2
July	29.0	29.0	—	—
August	31.4	20.0	27.8	46.3
Mean for year	35.5	32.4	37.0	41.8

It would thus appear that in the Gulf of Maine *C. finmarchicus* forms a more important member of the zoöplankton population than in the region off Möre, although at no time were eggs found in such quantities as reported from certain areas between Norway and Iceland, where Damas (1905, p. 12) found them at times comprising practically the entire haul. In the Gulf of Maine at the peak of June spawning (1932) eggs of *Calanus* were the dominant form, but were everywhere outnumbered by the combined eggs and larvæ of other species. In

the Bay of Fundy, also, Willey has commented (1921, p. 189) on the absence of *Calanus* eggs in any such relative abundance as reported by Damas. However, the importance of this species is evidenced by the manner in which the total volume of zoöplankton follows the fluctuations in the *Calanus* content (Fig. 2), a condition also noted by Ruud (1929, p. 12) for the Möre area.

Regional Distribution of the Adult Stock

The quantitative distribution of adult *C. finmarchicus* (including late copepodite stages) in the Gulf of Maine as described by Bigelow

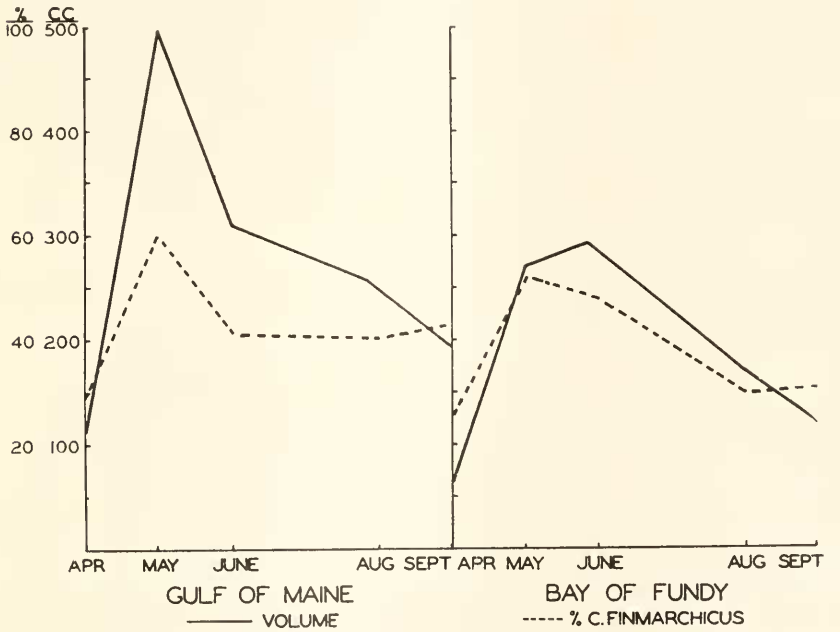

Fig. 2. Volume of zoöplankton and relative percentage by number of *C. finmarchicus* (adults and late copepodites) in the Gulf of Maine and Bay of Fundy in 1932.

(1926, p. 188) accords so closely with present data that little need be added here. Although almost everywhere abundant, Bigelow found marked horizontal variations. Together with other boreal plankton animals the smallest numbers were found in 1931 and 1932 in the Bay of Fundy, particularly on the New Brunswick side, and along the adjacent coast of Maine to Penobscot Bay. However, although the values were uniformly low, due to equally small numbers of other boreal zoöplankton species, *C. finmarchicus* is relatively almost as

important a member of the population in this region as elsewhere in the Gulf. The largest numbers in the Bay of Fundy occurred in the deep basin and along the Nova Scotian coast; in the Gulf of Maine, at the outer stations.

Production and Dispersal

Propagation of *Calanus finmarchicus* has been found to vary greatly in different localities, both in the rate of development and the number of broods. Available records indicate that in the southern portion of its range development is relatively rapid and spawning may begin as early as January. Proceeding northward into colder water, the period of vernal augmentation becomes increasingly later, development slower, and there are fewer broods.

In the Clyde Sea, a fairly enclosed basin with a mean annual temperature of over 10° C. and minimum holothermic temperatures in the spring of 5–7° C. (Chumley, 1918, p. 14),[3] eggs and nauplii of *C. finmarchicus* were found by Nicholls (1933, p. 89) in January,

Table II

Relative percentages by number of *C. finmarchicus* to population of total region of Bay of Fundy, and of Gulf of Maine in 1932.

1932	Total region	Bay of Fundy	Gulf of Maine		
			Total gulf	Western area	Central area
April	25.7	24.6	26.8	34.9	18.7
May	56.4	52.4	60.4	66.0	54.8
June	44.7	47.5	41.9	44.4	39.4
August	35.6	29.8	41.4	39.4	43.3
September	37.3	30.7	43.9	43.2	90.2
April–September	39.9	37.0	42.9	45.6	49.3

followed by three well defined breeding periods, February–March, April–May, and June–July, with additional subsidiary broods of lesser importance in July and August. These broods represent successive generations, the adults dying off after spawning.

In Norwegian waters off Möre, Ruud (1929) found propagation beginning in late March to early April, the maximum having passed by May both in 1926 and 1927. A second smaller maximum appeared in June and continued until late July. His records also indicate that spawning takes place earlier farther south and proceeds northward along the Norwegian coast where augmentation in spring and early

[3] In the Gulf of Maine there is a mean annual temperature of 7–8° C. and a minimum holothermic temperature of about 2° around the margin.

summer (April–June) had previously been reported (Gran, 1902; Damas, 1905; Damas and Koefoed, 1907, etc.).

In the region of Iceland, Paulsen (1906, pp. 19–20) reported the principal propagation season of *C. finmarchicus* to be from March until June with a possible second reproduction period later. At the meeting point of the Atlantic and North Polar currents, south of 67° N, the season is in late June (Damas, 1905), and east of Greenland, in late July (With, 1915).

In the Gulf of Maine and Bay of Fundy previous investigations have shown the stock of *Calanus* to be at a minimum in late February and early March, at which time regional differences would be expected to be least. Vernal augmentation begins in late March and April (depending on the locality) and varies somewhat from year to year. Early nauplii were abundant in Massachusetts Bay by April 7 in 1925 (Fish, 1928, p. 286). In coarse net hauls where the effect of production would not be noted until the new stock had reached copepodite stages, Bigelow (1926, p. 192) observed in 1920 a slight increase from March to April in the coastal zone between Cape Cod and Mt. Desert, a considerable increase in Massachusetts Bay (× 400), and in the western basin about the same average number as in February and March. His data of several years led him to conclude that probably the "multiplication of *Calanus* does not proceed so rapidly in the northern parts of the Gulf, though it may commence there as early as mid-April" (Ibid, p. 194). There was also evidence that breeding probably continues actively through June, and an increase in the numbers of *Calanus* in September suggested a second but less productive season in early autumn (Ibid, p. 207).

To the north Willey (1919) found evidence of vernal propagation over a broad area between Nova Scotia and Newfoundland. At the eastern end of St. Pierre Bank in 1915 *Calanus finmarchicus* in copepodite stages II–V was taken on June 24 and again on July 27. Stages III–VI were also obtained south of Cabot Strait on July 27 and in the Laurentian Channel on July 28.

Distribution of Eggs and Larvæ in 1932

An analysis of propagation in the Gulf of Maine and Bay of Fundy is complicated by the progressive delay in seasonal response from west to east (Fig. 3) combined with an active cyclonic drift, which renders it difficult to ascertain the source of larvæ taken in any particular locality. Fortunately an average difference of approximately one month in the time of spawning in the eastern and western parts of the Gulf made it possible to distinguish two breeding stocks, and, through the distribution of dominant developmental stages in successive

months, trace in a general manner the rate of growth and subsequent dispersal in each.

April.—Spawning must have begun in March, and by late April had terminated over the greater part of the Gulf. The more advanced

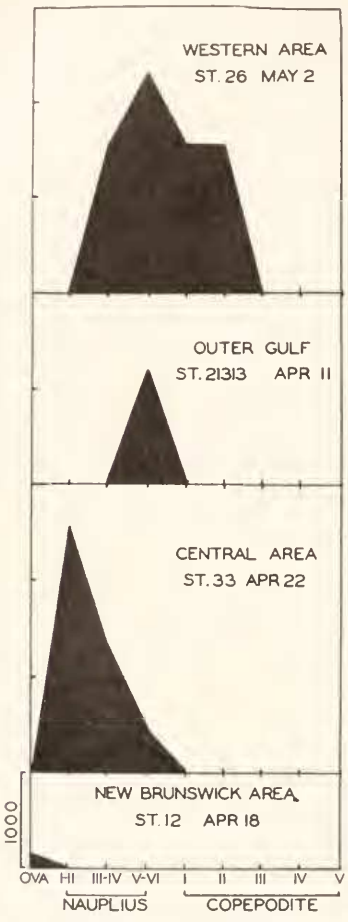

FIG. 3

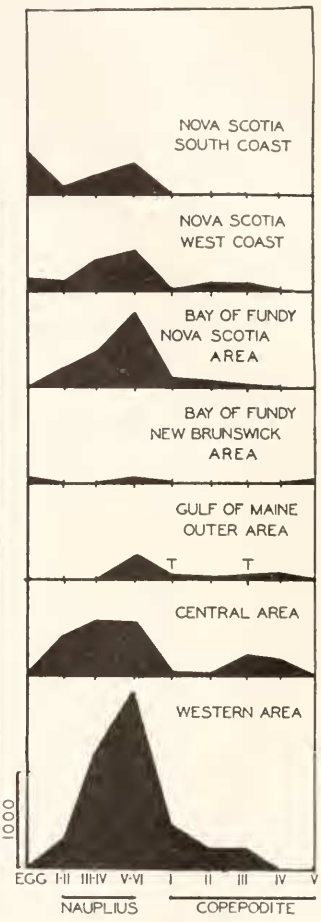

FIG. 4

FIG. 3. *Calanus finmarchicus*, showing progressive delay in seasonal response to the eastward, and evidence that the larval stock in the outer Gulf may have originated in the western area.

FIG. 4. *Calanus finmarchicus*, showing nauplius stages IV–VI dominating throughout the region in April 1932. (Average of all stations in each area.)

larvae had then reached the third and fourth copepodite stages, and were rather widely distributed in relatively small numbers. Nauplius stages IV–VI predominated in the Casco Bay region where production

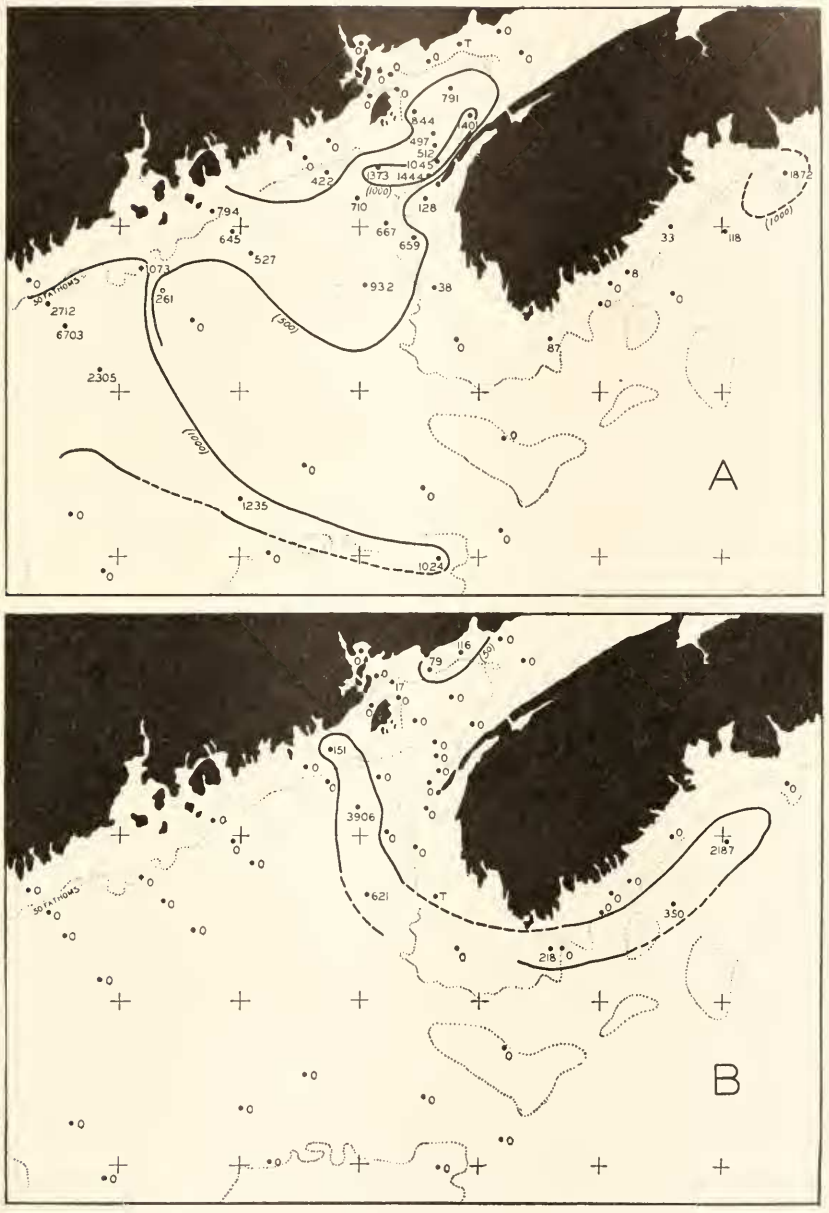

FIG. 5. Distribution of (*A*) nauplius stages V–VI of the western stock, and (*B*) eggs of the eastern stock in April 1932. Number per minute of towing.

was so much more extensive than elsewhere that its contributions outnumbered locally produced larvæ over the greater part of the Gulf and Bay, a condition which continued throughout the summer. As it was possible to make but one series of observations in the outer Gulf, the duration and extent of propagation in that area could not be determined, but the distribution of larvæ, consisting of nauplius stages V–VI with a small number of copepodite stage III and no intermediates, would suggest the western coastal area as the principal source. However, a local concentration of nauplius stages V–VI off Nova Scotia offers positive evidence that in outside waters the season was as far advanced off Halifax as in the region of Casco Bay. Between these two areas, along the south and west coasts of Nova Scotia, the season appeared to be less advanced, more closely corresponding to the eastern part of the Gulf where spawning had not yet ceased.

TABLE III

Maximal numbers of *Calanus finmarchicus* in various developmental stages in the western area of the Gulf and the Bay of Fundy, May, 1932.

Locality	1932	Ova	Nauplius			Copepodite				
			I–II	III–IV	V–VI	I	II	III	IV	V
Western area (Station 26)	May 31			1029	515	1029	3603	8234	4117	2058
Bay of Fundy (Station 36)	May 22	669	1338	6021	8697		1338	669		

Eggs of the eastern breeding stock were found in varying abundance in the central area, the Bay of Fundy, and off the west and south coasts of Nova Scotia, but not west of Mt. Desert or in the vicinity of Georges Banks.

May.—By the latter part of May, as indicated in Table III, the maximum numbers of larvæ from the western area were in copepodite stage III, and the local crop east of Mt. Desert, in nauplius stages V–VI, the latter corresponding to conditions in the western area a month earlier. In Fig. 6A late larval stages are seen to extend eastward from the rich Casco Bay region in a band whose inner margin parallels the 100-meter contour. They also penetrated in a tongue-like wedge into the Bay of Fundy along the Nova Scotian side, and show as a distinct second maximum in curves from both the Fundy and central areas (See Fig. 8, May sections off Cape Spencer, and Mt. Desert; also Table III, Station 36). These late copepodites of *Calanus finmarchicus* now dominated the total population and accounted largely for the tremendous rise in the volume of zoöplankton from April

to May (Fig. 2).[4] Due to dispersal from the western area volumes everywhere increased, the increase being least noticeable in areas where

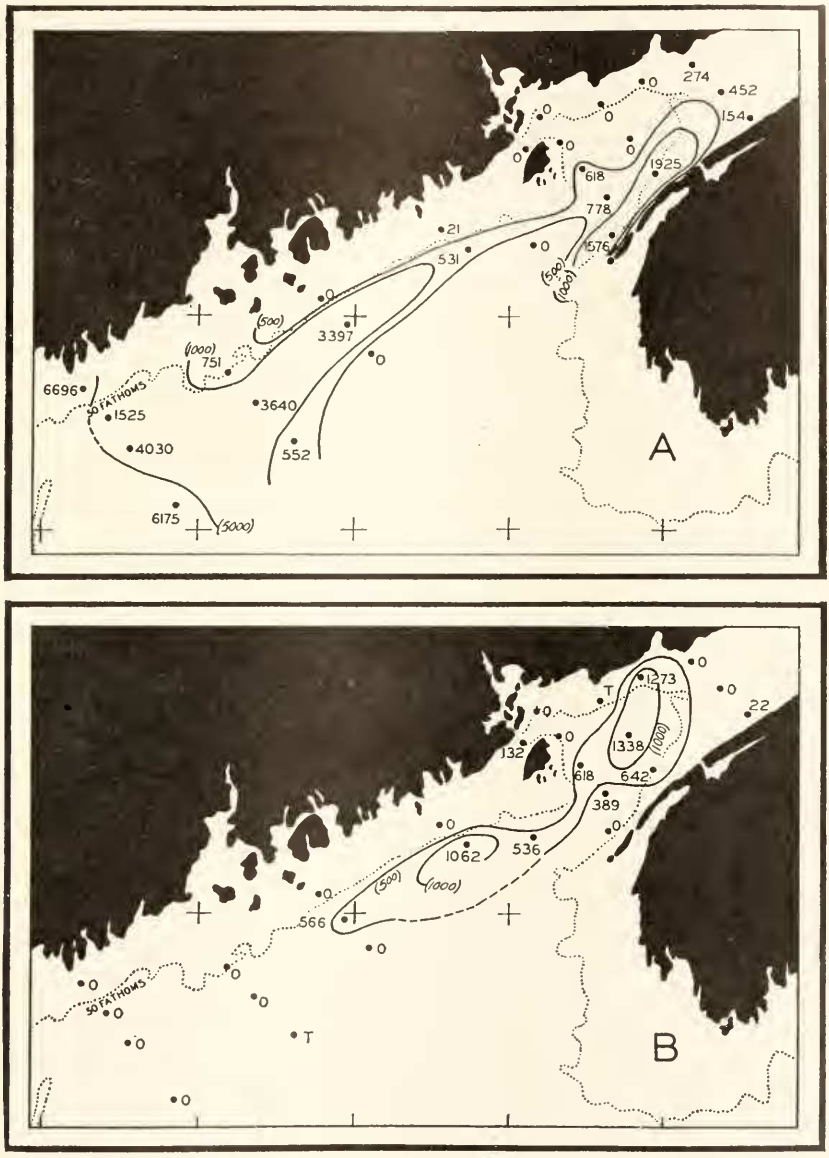

FIG. 6. Distribution of (*A*) copepodite stages IV–V of the western stock, and (*B*) nauplius stages I–II of the eastern stock in May 1932. Number per minute of towing.

[4] Bogorov (1933) records an increase in the biomass (weight) of almost 60 times from copepodite stage I to stage VI.

the immigrant stock was not supplemented by a significant amount of local propagation. Particularly in the eastern coastal and New Brunswick regions, individuals of the local brood were not of sufficient size to be taken in the coarse meter nets in May.

Although late nauplii dominated in the eastern Gulf stock, some spawning must have continued well into May in the coastal waters east of Petit Manan, because early nauplii (I–II) were still numerous in this region between May 18 and 24 (Fig. 6*B*).

June.—The first western crop had matured and were spawning by June 20. As eggs were everywhere abundant (Figs. 7*A* and 8), although the eastern brood was still in copepodite stages (Fig. 9), the parent stock in all probability consisted almost entirely of individuals dispersed from the western area. In the eastern basin it is possible that the adults breeding at this time may have been reinforced to some extent from production centers outside of the Gulf, a possibility suggested by Bigelow's (1926, p. 209) records of a swarm of adults in this region on May 6, 1915, and the fact that in 1932 the largest single capture of eggs (25,321 per minute) was made in the eastern basin in June.

The eastern spring brood, in copepodite stages in June (Fig. 7*B*), were most numerous off Penobscot Bay and along the course of the drift into the Bay of Fundy. Elsewhere in the Bay and over the greater part of the central area, no copepodite stages were found, indicating that this brood suffers heavy mortality and only those produced in or transported as far as the western part of the central area survive.

August.—On August 11 in the Casco Bay region, after an interval of 42 days, the product of June spawning of the western stock, now in copepodite stages (III predominating), had been largely dissipated and the relatively few taken were distributed along the outermost stations from Casco Bay to the eastern basin. Elsewhere in the Gulf and Bay their numbers were extremely sparse.

Contrasted with copepodites of this second western crop, eggs and early larvae, assumed to represent spawning by the first eastern brood, were concentrated nearer the coast. Early nauplii were most abundant in the Bay of Fundy (Station 7) and central area, with smaller numbers occurring westward at the inner stations to Casco Bay.

September.—It was not possible to obtain data from the Gulf of Maine in September, but stations in the Bay of Fundy yielded small numbers of eggs, early nauplii (stage I) and copepodites in stage II. The latter were probably the product of August spawning by a second eastern brood and the former, in view of the absence of eggs and early

larvæ along the New Brunswick coast and their concentration in the course of the drift along the Nova Scotian coast and over the deep basin in the Bay of Fundy on September 15, suggest a third generation of the western stock entering from the Gulf.

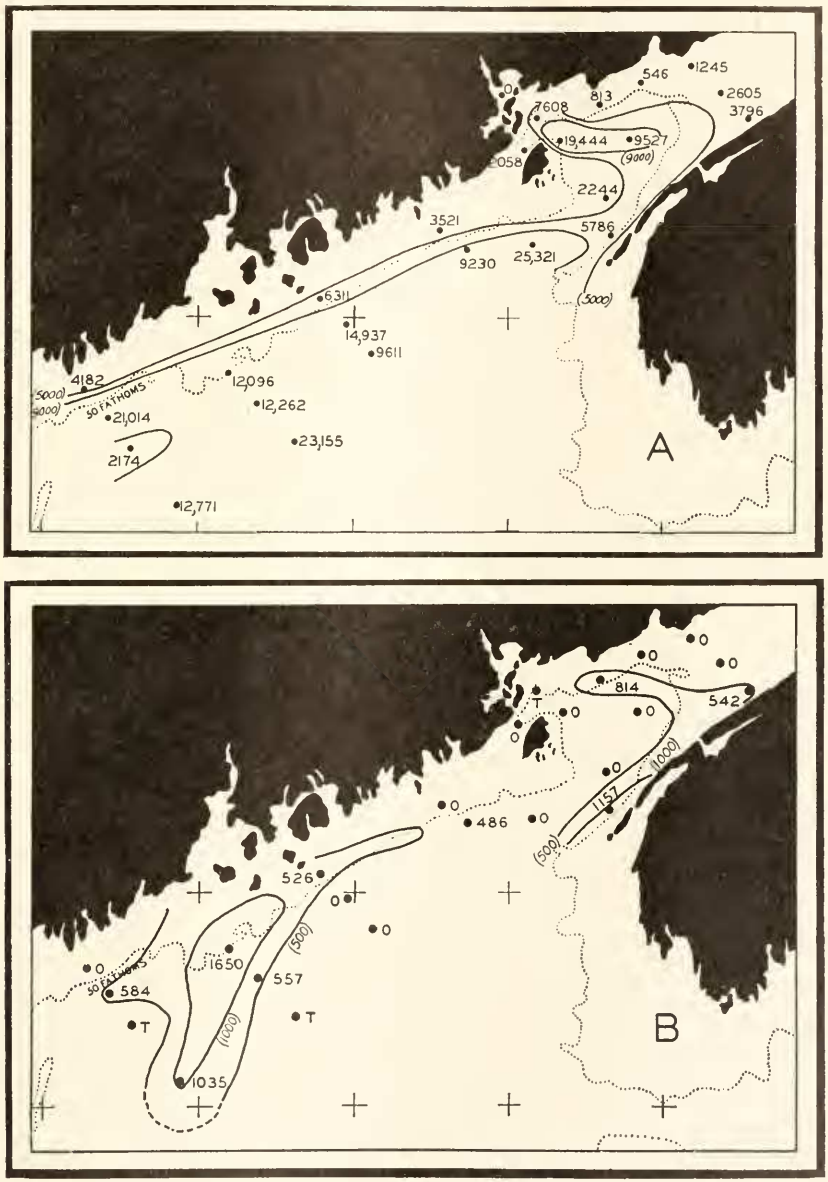

FIG. 7. Distribution of (*A*) eggs of the western stock, and (*B*) copepodite stages I–V of the eastern stock in June 1932. Number per minute of towing.

Comparison of Results in 1931 and 1932

In 1931 but one set of observations was made in the Gulf and Bay (August 21–September 5), corresponding stations being taken about two weeks later than in 1932 (August 8–21).

The season appears to have been about the same in the western area during the two years because a maximum of eggs between August 11 and 14 in 1932 would undoubtedly have hatched by August 21 when early nauplii were found predominating in 1931.

East of Mt. Desert, as the relative percentage of eggs and nauplii were much the same in the Nova Scotian and New Brunswick areas on August 17–21 in 1932 as on September 1–5, the spawning season would appear to have been about two weeks later in the previous year. Not having hydrographic data from the eastern basin of the Gulf for 1931, it is not possible to suggest a reason for the retarded season that year. Temperatures within the Bay of Fundy in 1931 and 1932 were not substantially different at this time.

Discussion and Conclusions

Throughout the Gulf of Maine and Bay of Fundy propagation begins in the spring and is followed by a succession of generations until autumn. The marked regional differences in the time when vernal augmentation begins are reflected through succeeding generations of that summer, irrespective of where the stock may become distributed. Thus by the time (June) that the spring crop from the western area has matured and spawned, it has become so generally distributed that eggs appear almost simultaneously throughout the Gulf and Bay (Fig. 8). Again, in July and August, when the smaller eastern vernal crop spawns, eggs appear in even greater abundance in the western area than in the region where the stock originates.

Propagation of the Stock Originating West of Mt. Desert in the Spring

The seasonal distribution of eggs and larvæ indicate two clearly defined spawning periods, March–April and June–July with a possible third in September. It is probable that most of the June–July brood remains in copepodite stages to form the bulk of the winter stock (maturing the following spring), but some appear to pass through the final moult and spawn in September.

The maximum numbers of larvæ of the first generation, which by late April in 1932 were in nauplius stages IV–VI, and in copepodite stage III thirty days later, had matured and were spawning by June 20.

The second generation is not as clearly traceable, but what are believed to have been members of the June brood were mainly in copepodite stage III forty-five days later on August 11 (Fig. 8, section *A*), and some became spawning adults by September 15 (p. 129).

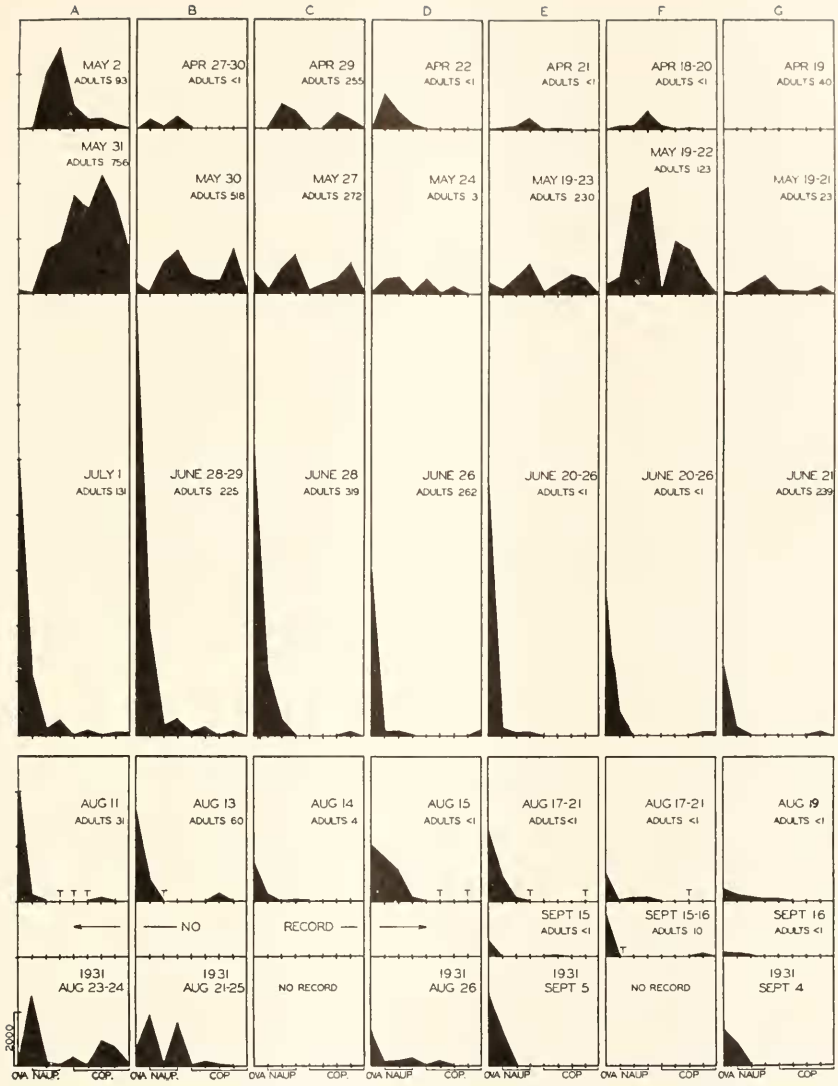

FIG. 8. Seasonal changes in the composition of the population of *Calanus finmarchicus* (developmental stages) in seven sections between Casco Bay and Cape Spencer.

Stages recorded as ova; nauplii I–II, III–IV, V–VI; copepodites I, II, III, IV, V.

Sections: *A*. Casco Bay (Stations 23*A*–25*A*, 26)
B. Penobscot Bay (Stations 27–29)
C. Mt. Desert (Stations 17, 30–31)
D. Moose Peak (Stations 32–33)
E. Passamaquoddy Bay (Stations 5–8*A*, 35)
F. Pt. Lipreau (Stations 13, 36–37)
G. Cape Spencer (Stations 9–11).

April–June: number per minute of towing.
August–September: number per cubic meter.

Propagation of the Stock Originating East of Mt. Desert

This region (Fig. 1) shows considerable local variation. In its western portion approaching Mt. Desert and on the Nova Scotian side of the Bay of Fundy (influenced by inflow from the outer Gulf), the spawning seasons of *Calanus* more closely approximated those to the west of Mt. Desert, while along the coast eastward from Petit

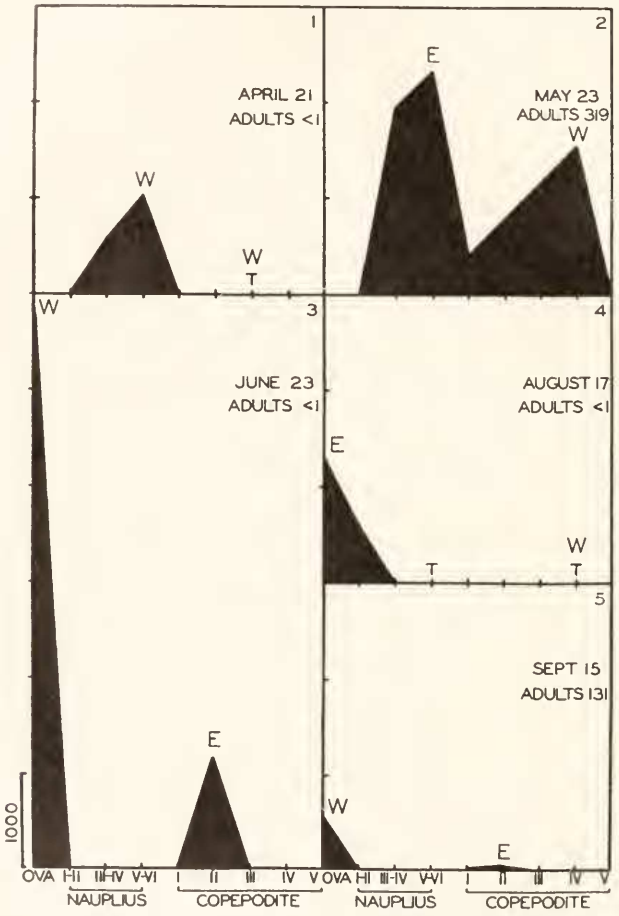

FIG. 9. Development of the western (*W*) and eastern (*E*) stocks as indicated at station 8.1 in the drift entering the Bay of Fundy in 1932.

Manan to St. John the seasons were progressively later. However, although evident, these local seasonal differences are relatively small, and for present biological purposes the waters east of Mt. Desert can be considered to comprise one region in which the maxima of corresponding stages of *Calanus* occur, as previously noted (p. 123), about four weeks later than in the western part of the Gulf.

There appear to be two less well defined propagation periods of the eastern stock, April–May and July–August. The first is indicated by eggs appearing along the New Brunswick coast on April 18 (Fig. 3) and the maximum of nauplius stages I–II in the vicinity of Petit Manan (Station 33) on April 22 (Fig. 3). Reaching nauplius V–VI a month later (May 18–24) and copepodite stages II–IV on June 20–26 (Figs. 8 and 9), it is presumed that August (8–21) eggs represent spawning by adults of this stock.

It was not possible to trace with certainty the outcome of July–August propagation because of the small number of individuals involved, but it would appear that the copepodites (stage II) entering the Bay of Fundy on September 15 (Fig. 9) were representatives of this crop. This second eastern brood of copepodites probably supplements the second and third (?) western broods to form the winter stock.

Rate of Early Development

In the Clyde Sea (Nicholls, 1933, p. 92) field and laboratory records have indicated a maximum of four weeks for the complete development of *Calanus finmarchicus*, a minimum of eleven days between the egg and first copepodite stage and intervals of three days for successive moults to stage V. A minimum of four days was required for the final moult to stage VI (adult).

Lebour (1916, p. 9), in laboratory experiments at Plymouth, found that nauplii appearing between April 17 and 24 reached copepodite stage V on May 19, having taken less than two months for development from the egg to the latter stage.

Off Möre Ruud (1929, p. 38) estimates that *Calanus finmarchicus* requires almost three months for its life cycle, allowing three to four weeks for embryonal development as indicated by Lebour (1916, p. 9). In 1926 there was about seven weeks between the maximum of nauplii and the maximum of stage VI.

In the Gulf of Maine the developmental period appears to be slightly less than in Norwegian waters, but, as observations at each station were taken at minimum intervals of one month, the rate of growth can only be approximated. In the case of the western stock, with an interval of 29–33 days between the maximum of copepodite stage III in May and the presence of eggs in June, followed by a period of 42–46 days before the next maximum of copepodite stage III, the complete cycle would appear to require from 71–79 days. Again, if eggs observed on September 15 (p. 129) can be considered to represent spawning by individuals incubating west of Mt. Desert from June 28 to July 1, and in copepodite stage III on August 11–14, then there

must have been a maximum period of approximately 78–81 days between the second and third broods of eggs.

The two generations of the western stock would thus agree rather well and suggest a period of about two and one-half months from the egg to the spawning adult. Intervals between maxima of different stages also indicate about one month for the development from nauplius I to copepodite I, one-half month from copepodite I to copepodite V, and one month for the final moult, maturation, and incubation of the eggs. Although requiring confirmation by laboratory experimentation, there would seem to be about five days between moults in the nauplius stages and three days in the copepodite stages.[5]

No attempt has been made to calculate the developmental period of the eastern stock, hatching shortly before April 22 in the central area (Fig. 3, Station 33), because the greater part of this brood apparently matured and spawned in July, between cruises, and eggs taken in August no doubt represent late season spawning. This is indicated by the large percentage of nauplii up to stages III–IV in the central area on August 15.

August 15, 1932	Ova	Naup. I–II	Naup. III–IV	Naup. V–VI	Cop. I–V
Central area (Station 33)	3,390	1,507	2,450	377	T

The rate of development would appear to be substantially the same as in the western stock, which is not surprising in view of the evidence that those members of the eastern spring brood reaching maturity probably entered the western area in early stages.

Rate of Late Development

As there was an interval of about one month between the maximum of late copepodite stages III–IV (May 27–31) and the next maximum of eggs (June 28–July 1) in the area west of Mt. Desert, it would appear that the time required for the ripening of the gonads and fertilization, after the moult to stage VI (adult), is probably about three weeks. A similar interval is suggested by the June brood if copepodite stages III–IV from the western region (August 11–13) formed the parent stock of early eggs entering the Bay of Fundy on September 15–16 (Fig. 8) in 1932. Nicholls (1933, p. 95) found that, having moulted to adults, there is a lag of from three weeks to one month before the next maximum of eggs in the Clyde Sea.

[5] At Station 8.1 copepodite stage II predominated on May 15, and copepodite stage IV on May 23, nine days later.

Data on the interval between the final moult and the time of spawning in the winter stock are available only for the Bay of Fundy. Here the period must be considerably longer than in succeeding generations in the Gulf. The winter population, almost entirely in late copepodite stages in November, is indicated in Table IV and also in a haul by Willey in Passamaquoddy Bay (1921, pp. 187–8) on November 2 in 1916 when copepodites in stage V formed 46 per cent and adult females only 2 per cent of the total macrocalanid plankton. By February 23 in 1917 adult males and females formed 47 per cent and copepodite stage V, 36 per cent. In 1932, as shown below, the winter stock in this area had almost completed moulting (97.6 per cent adults) by March 21 and a considerable proportion of the females contained developing eggs. Yet no eggs were found in these waters on April 15, and spawning had apparently just begun on May 5.

TABLE IV

Winter population of *C. finmarchicus* in Bay of Fundy. Percentages by number of various developmental stages to total zoöplankton population.

Date	Copepodite		Adult	
1931–1932	Stage IV	Stage V	♀	♂
November 16	3.8%	96.2%	0%	0%
March 21	0%	2.4%	92.9	4.7

Relative Abundance of Adults

Accurate figures on the relative number of adults and individuals in developmental stages are difficult to obtain because the former cannot be sampled in a representative manner with the apparatus required for eggs and early larvæ. Copepodite stages IV and V, however, appear to have been sampled efficiently with both the coarse and fine nets, and by taking the fine net counts and applying the meter net data on the relative percentage of these stages to adults, it has been possible to obtain roughly comparable figures for the latter. Similar figures have been obtained for August and September using pump and meter net data but the error may prove to be greater in this case if it is found that late larvæ, particularly copepodite stage V, cannot be sampled representatively with the pump. There is some evidence that this might be true, in which event the mean number of both adults and late copepodite stages in the total region would be somewhat larger than indicated in Table V.

Mortality among Maturing Adults

In the Gulf of Maine during the interval between the maximum of late copepodite stages in late May and the maximum of eggs in June, there occurred the highest rate of mortality observed in zoöplankton during the year, the decline in the relative percentage of *Calanus* exceeding even the tremendous decline in the total volume of animal plankton (Fig. 2) at a time when the spring stock of this species, just reaching maturity, might have been expected to substantially increase the total plankton volume (p. 128).

A similar decline in *Calanus* in the Clyde Sea (where, as in the Gulf of Maine, the maximum of eggs coincides with the minimum of adult females) has been interpreted by Nicholls (1933, p. 95) to indicate that the period of maturation forms a very critical time during which the rate of mortality is so high that comparatively few females survive.

Support for this interpretation was found in the Bay of Fundy, where the eastern vernal crop was still in copepodite stages in late June. If the decline from May to June is not primarily due to a depletion of the food supply or unfavorable physical conditions, excessive mortality in the Bay would at this time be limited to immi-

TABLE V

Number of *C. finmarchicus* in various stages of development, April to September, 1932.

1932	No. stations	Method	Eggs	Nauplii	Copepodites	Adults
April	27	Net	4	1615	406	128
May	26	Net	301	3013	4138	319
June	26	Net	8432	1850	307	311
August	27	Pump	2158	882	69	21
September	12	Pump	753	7	35	4

Net: number per minute. Pump: number per cubic meter.

grants from the west. Figure 2 shows this to be the case, as the eastern stock apparently offsets the decline of western immigrants in the Bay, and the mean volume continued to increase through June.

Mortality in maturing adults of subsequent generations in the Gulf and Bay was not as clearly evident because both the meter net and pump data indicate that comparatively few survived to reach even copepodite stages. Perhaps the greater number of predatory plankton animals in summer served to keep the numbers down. Some such explanation is necessary to account for the large crop derived from the relatively small parent stock in March–April as compared with that in May–June.

Length of Life of Different Broods

The marked decline in the relative percentage of adults to copepodites following the breeding period in June (Fig. 10*A*), in view of the fact that in relation to eggs and nauplii, copepodites showed no signifi-

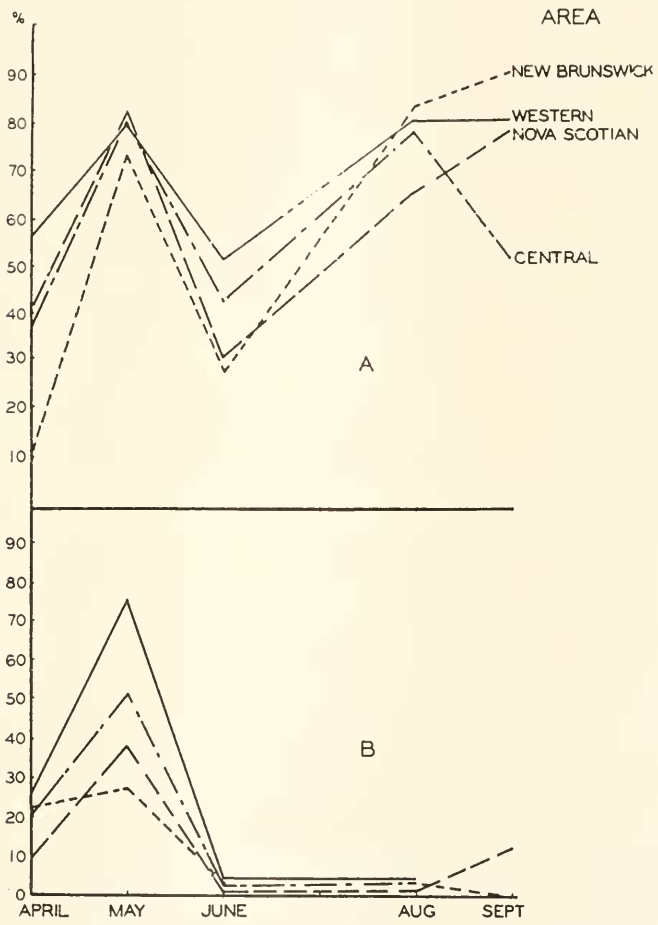

FIG. 10. *Calanus finmarchicus.* Seasonal changes in the relative percentage of (*A*) copepodites to adults, and (*B*) copepodites to eggs and nauplii.

cant increase (Fig. 10*B*), is considered to represent a dying off of adults after spawning. This appears to be a rather well-established characteristic of the species in the eastern Atlantic (Damas, 1905; Paulsen, 1906; Nicholls, 1933) and has been suggested by Bigelow (1926, p. 206) in the Gulf of Maine.

The length of life of individuals produced in early April and maturing in June would thus probably not exceed four months, allowing two and one-half months for development to maturity and a maximum of one and one-half months of adult life (spawning adults in the western region on June 28–July 1 had greatly diminished by August 11–14 in 1932). A similar period of adult life in spring and summer (one and one-half months) has been found by Nicholls in the Clyde Sea area (1933, p. 92).

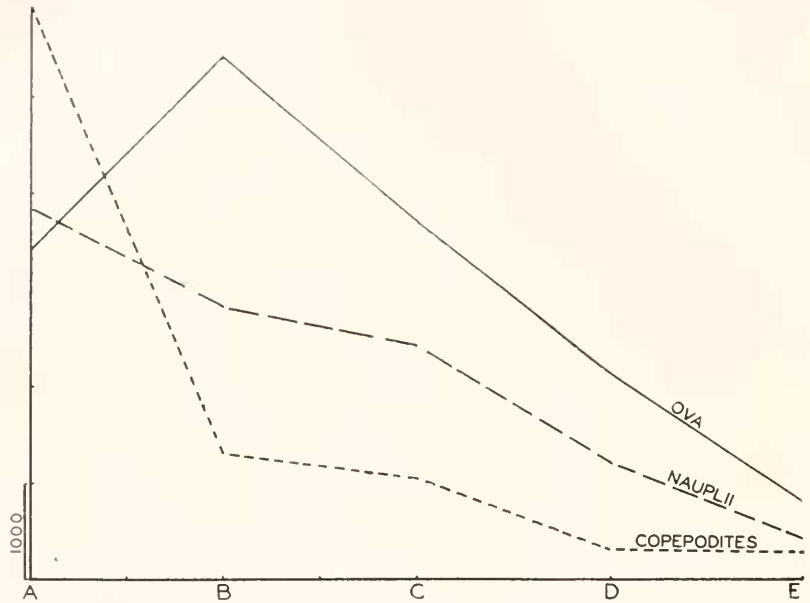

FIG. 11. Mean numbers of ova, nauplius and copepodite stages per minute of hauling for the period April–July, 1932.
Sections: *A*. Casco Bay, *B*. Penobscot Bay, *C*. Mt. Desert, *D*. Moose Peak, *E*. Cape Spencer.

In regard to the winter stock, in cold areas with fewer generations the length of life must be longer than in regions such as the Clyde Sea where spawning begins very early in the year. Our data would indicate that the increase in the number of copepodites in September, observed by Bigelow (1926, p. 207) in the Gulf and in 1932 in the drift entering the Bay of Fundy (increased from 0.3 per cent to 13.6 per cent, Fig. 10*B*), represented arrested development of at least a part of the June crop from the western region, supplemented perhaps to some extent by the July-August crop from the waters east of Mt. Desert. The small numbers of eggs of the third western brood in September do not appear adequate to account for the winter population. If the

winter group then consists largely of individuals produced in June–August and dying off after spawning the following March–April, a maximum existence of approximately 10–11 months is indicated. September-spawned *Calanus* would have a maximum existence of 7–8 months. In the Bay of Fundy the period must be even longer (p. 133). Nicholls estimates (1933, pp. 91–92) the length of life of *Calanus* in the Clyde Sea area to be about nine weeks after the winter group has moulted to stage VI, with a total existence of 7–8 months.

There is some evidence that after reaching maturity the males of *Calanus finmarchicus* die off some time before the females. Referring again to Willey's records from the Quoddy region (1921, p. 187), of the adults taken on February 23 in 1917, males formed 20 per cent and females 27 per cent. In 1932 on March 21, a month later, females formed 92.9 per cent of the *Calanus* stock and males 4.7 per cent. Damas (1905) also found males of this species rare except at the epoch of vernal reproduction.

TABLE VI

Number of *C. finmarchicus* found in different stages in the New Brunswick area, April to September. April–June, number per minute. July to September, number per cubic meter.

New Brunswick area	Station	Ova	Nauplius			Copepodite				
1932			I–II	III–IV	V–VI	I	II	III	IV	V
April 15	5									
May 4	5	17								
May 19	5			31	62					
June 20	5	7608		507	507				T	
July 30	5	710	140							
August 21	5	375	187							
September 16	11A		40							

Relative Importance of Different Spawning Areas

The contention of previous observers (Willey, 1921, p. 189; Bigelow 1926, p. 207) that the western Gulf probably forms the principal source of supply of *Calanus* for the entire region, is borne out by the present investigations. At all times the coastal region west of Mt. Desert yielded the greatest numbers of eggs, larvæ, and adults, and the rapid decline to the eastward (Fig. 11), combined with the distribution of larvæ, designate it as the probable source of the major part of the population in the outer Gulf, the central area, and the Bay of Fundy. The fluctuations in the mean volume and relative percentage of *Calanus* in the total region in 1932 paralleled the seasonal changes in the western area (Fig. 2).

No doubt a portion of the individuals produced in the eastern region, particularly near its western margin, survive because the stock in very small numbers can be traced through successive generations. However, over the greater part of the Bay of Fundy and the turbulent coastal region of the Gulf east of Petit Manan, there is no evidence of any successful production of *Calanus*, although eggs transported west from the latter area may complete their development in a more favorable environment.

In the Quoddy region (Station 5), somewhat removed from the path of the drift from the Gulf, hauls throughout the season consisted principally of eggs with relatively few nauplii. Copepodite stages were taken during the summer with a meter net but their numbers were so small that almost none were found in pump and fine net samples. The large brood produced by immigrant adults in late June had apparently entirely vanished a month later, and eggs of the eastern stock in late July and August seem to have disappeared by September 16. A similar condition was found in August and September, 1931.

Summary

1. *Calanus finmarchicus* is the most abundant pelagic animal in the Gulf of Maine, averaging 39.9 per cent of the total zoöplankton population during the period April to September, 1932, with a peak of 60.4 per cent in May. In the Bay of Fundy there was a mean of 35.5 per cent for the year 1931–32.

2. The adult stock varies markedly in abundance in different areas, the smallest numbers occurring in the Bay of Fundy and westward along the coast of Maine to Penobscot Bay. The population is everywhere at a minimum in late February and early March.

3. *Calanus* passes the winter largely in copepodite stage V, the final moult taking place in February and early March shortly before vernal augmentation.

4. An average difference of approximately one month in the time of spawning in the eastern and western parts of the region is reflected in succeeding generations after dispersal. Two breeding stocks can thus be distinguished.

5. In the western stock there are two well-defined breeding periods, March–April, and June–July, with a possible third in September, and two periods, April–May, and July–August in the eastern stock.

6. A developmental period of two and one-half months is indicated in both stocks, one month from nauplius I to copepodite I, one-half month from copepodite I to copepodite V, and one month for the final moult, maturation, and incubation of eggs.

7. Mortality is highest among maturing adults.

8. The total length of life in spring and summer does not exceed four months. The winter stock has a maximum existence of 10–11 months.

9. After reaching maturity the males die off before the females.

10. The western Gulf forms the principal source of supply of *Calanus* for the entire region. Propagation east of Mt. Desert in the inner Gulf is largely if not entirely, unsuccessful.

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